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Mass disease and mortality of Baikal sponges

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ABSTRACT. In recent years, significant changes in the ecological system of the coastal (littoral) zone, including mass death of the endemic representatives of the freshwater sponges of the Lubomirskiidae family, have been an urgent problem of Lake Baikal. Similar problems are known all over the world. Thus, mass disease and death of corals and sponges are indicated in the Mediterranean, Adriatic, Caribbean and other seas, which raises serious concerns about the future of these biocenoses (Olson et al., 2006; Webster, 2007; Wulff et al., 2007; Stabili et al., 2012). In Baikal, diseased sponges were first found in 2011. The area of sponge disease is constantly expanding, and, to date, dying specimens have been found throughout the lake. The mass death of sponges occur in presence of the large-scale violation of the spatial distribution and the structure of phytocenoses in the littoral zone, but the causes of these phenomena are unknown.

The relevance of the problem arises from the fact that changes in the littoral zone of Lake Baikal can significantly affect the productivity and composition of planktonic organisms and zoobenthos, which are the food base for fish, as well as the quality of drinking water. The deterioration of the ecological state also affects the attractiveness of the lake for tourism. At the international level, serious intellectual and financial resources were mobilized to solve similar problems. Despite the obvious relevance, in Russia such studies are carried out irregularly by small groups of researchers.

Keywords: Baikal, sponges, mass death, metagenome, dysbiose

1. Introduction

Lake Baikal is sometimes called The Galapagos Islands of Russia because of its exceptional biodiversity and importance for the evolutionary science. The age, isolation and deep oxygen-saturated waters of Lake Baikal formed one of the world's richest freshwater ecosystems. Lake Baikal located in the centre of Eurasia has many features inherent to the ocean: abyssal depths and a huge mass of water, internal waves and seiches, strong storms and high waves, upwelling, expansion of the basin due to the separation of the coast similar to the separation of the continents of Africa and South America, large magnitudes of magnetic anomalies, etc. (Kondratyev, 1992). Lake Baikal is the only deep-water lake, where the water saturated with oxygen stretches to the very bottom, like in the ocean.

The ecosystem of Lake Baikal is also close to oceanic ecosystems by structure and other characteristics, e.g. the presence of a pelagic community of the organisms and zones with high productivity of macroplankton in the area of the slope similar to the highly productive zones of upwelling in the ocean. The benthic community is characterized by extraordinary species diversity and high production, and it mainly consists of oligochaetes, molluscs, amphipods, chironomids and sponges. The biomass of sponges exceeds tenfold the biomass of all littoral macroorganisms (Kozhov, 1972; Masuda, 2009).

The biological diversity of plants and animals inhabiting Baikal is greater than in other lakes of the world. For example, the number of known species and subspecies is more than twice higher than in Lake Tanganyika, which is comparable to Baikal in dimensions and origin. At present, there are approximately 2500 species of animals and more than 1000 species of plants in Lake Baikal. The Baikal fauna is formed autochthonous, i.e. the diversity of endemics has developed in Lake Baikal itself. Baikal is one of the most transparent lakes in the world. The amazing transparency (approximately 40 meters) has resulted from the low content of mineral salts in the lake and a great filtering ability of sponge communities and other filtration organisms.

Recently, Lake Baikal is facing increasing threats to environment. Global climate change can threaten its

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ecosystem; thus, the temperature of the surface water layers and the ice cover have already changed. Other threats are the industrialization of Russia and Mongolia, as well as the explosive boom of tourism. The huge increase in tourists on the shores of the lake does not lead to a real understanding by the authorities of how the waste products of tourists affect Baikal, and the locals do not have the adequate waste management systems for the tourist business. However, the largest threats are the changes in the biological community of the coastal zone.

Thus, the abundant growth of the filamentous algae *Spirogyra* was first recorded in 2010 in Bolshiye Koty Bay, which subsequently spread to other areas (Timoshkin et al., 2014). Mass reproduction of Spirogyra is found in shallow water, in areas with an increased content of biogenic elements. Filaments of dying off algae are washed out in shallow water, where they rot releasing the toxic substances uncharacteristic for the lake that affect the water quality.

Almost simultaneously with the onset of the abundant growth of the filamentous algae in the littoral zone of the lake, diseased sponges of anomalous pink colour were found. The disease of freshwater sponges in Lake Baikal first appeared in 2011 (Bormotov, 2011) and was accompanied by the death of the symbiont green microalgae changing the green colour of the sponges to pink. Sponges with anomalous colouration were found only in Central Baikal at depths of 25-55 m. In subsequent years, the external signs of the disease changed, and now sponges are found throughout the lake with different symptoms of body lesions, such as discolouration, tissue necrosis, the formation of brown plaque and dirty purple bacterial covers of separate branches. The number of sponges *Lubomirskia baicalensis*, which are the most sensitive to the disease, reduced by a third. In addition, 10-20% of annually registered sick sponges died during winter (Timoshkin et al., 2016; Khanaev et al., 2018).

2. Analysis of diseases of marine sponges

Healthy sponges are in dynamic equilibrium between the macroorganism, symbiotic microorganisms and microorganisms from the environment, the quantitative and species composition of which can vary greatly during drastic changes. The impact of stress on sponges can cause dysbiosis, i.e. a violation of the symbiotic community. In sponges, it is often characterized by increased alpha diversity (Luter et al., 2012) or the appearance of opportunistic pathogens (Simister et al., 2012). The stress can threaten the physiology and immunity of the host (Ghanbari et al., 2015; Pinzón et al., 2015; Liu et al., 2016), which further leads to loss of control of the microbiome and death of sponges. Thus, dysbiosis is probably not the cause of the disease, but may be a response of sponges to stress.

Recently, an unprecedented increase in the number of diseases of benthic organisms, including sponges, corals and algae, has been observed worldwide (Webster, 2007; Bourne et al., 2009; Burge et al., 2014), some of which led to mass mortality (Garrabou et al., 2009). For example, in the Mediterranean in 2008 and 2009, 80-95% of *Ircinia fasciculata* and *Sarcotragus spinosulum* samples died. The sponge disease *Ianthella basta* and *Rhopaloeides odorabile* was widely spread on the Great Barrier Reef (Luter et al., 2010a; 2010b). From the latter sponge, the pathogenic strain NW4327 *Pseudoalteromonas agarivorans* was isolated (Webster et al., 2002; Choudhury et al., 2015). However, in many other studies, only an imbalance of microorganisms was found causing a greater variety of microorganisms in diseased sponges in comparison with healthy individuals. The disease was accompanied by the development of opportunistic, often polymicrobial infections (Lesser et al., 2007; Coma et al., 2009; Bourne et al., 2016). In most cases, researchers only state dysbiosis, i.e. a shift in the microbial community of diseased sponges, without isolating a pathogenic agent (Webster et al., 2008; Gao et al., 2015; Blanquer et al., 2016; Luter et al., 2017; Deignan et al., 2018).

At present, symbiotic communities consisting of a host macroorganism (animals, plant and algae) and its associated microflora have been proposed to be called holobionts, a complex ecosystem, which symbiotic partners are closely interrelated by functions that cannot be performed by individual organisms (Rohwer et al., 2002; Bosch and McFall-Ngai, 2011; McFall-Ngai et al., 2013; Bordenstein and Theis, 2015). Only a single harmonious system of host, together with symbiotic microorganisms, ensures interaction with the environment and affects the health and functioning of the entire ecosystem. Sponges are one of the most diverse and complex aquatic habitat holobionts.

Sponges are simple, but successful organisms, which evolutionary age exceeds 600 million years, and they are common everywhere (Van Soest et al., 2012; Maldonado et al., 2015). Sponges are sessile organisms that filter large amounts of water for nutrition (Gili and Coma, 1998; de Goeij et al., 2013; Kahn et al., 2015; Maldonado et al., 2015); therefore, they are strongly affected by waterborne viruses, bacteria, archaea and eukaryotic microorganisms (Thomas et al., 2016; Moitinho-Silva et al., 2017). These microorganisms are the main source of food for sponges, but, at the same time, there are various symbiotic microbial partners in the body of sponges that have avoided the effects of the immune system. Microbial communities contribute to the nutrition, protection, immunity and development of the host, collectively affecting its functioning and health (Koropatnick et al., 2004; Eberl, 2010; Nicholson et al., 2012; Flórez et al., 2015). Symbionts of sponges are species-specific and are divided into two clusters: the core microbiome consisting of microorganisms found in most species of sponges, and the variable microbiome consisting of ‘focused specialists’, which differ in their relative numbers and are rarely found in other species (Erwin et al., 2012; Hester et al., 2015; Thomas et al., 2016). Unfortunately, the formation patterns of these two groups remain unknown (Moitinho-Silva et al., 2017). A sponge holobiont is a dynamic ecosystem that reacts to changes in the environment, particularly, anthropogenic stressors that threaten the holobiont stability and lead to dysbiosis, illness and death of sponges.

So far, the causes of death among sponges and other sessile filtering organisms recorded worldwide are not precisely known, and methods of combating this phenomenon, as well as ways to prevent it have not been found. Recently, methods of a next-generation sequencing and analysis of interactions in the host-microorganism system have been widely used to study the diversity of eukaryotic microbial symbionts and ways of structuring microbial communities (Costello et al., 2012). In the study of diseases and death of sponges and corals, metagenome sequencing is most often used to study changes in the composition and activity of bacterial communities. The key unresolved problem is whether the functional features of symbiotic microorganisms can be predicted based on their taxonomic position. Understanding of these ecological problems will provide answers to long-standing evolutionary questions, particularly, whether microorganisms can influence speciation models and evolutionary diversification of their hosts (Brucker and Bordenstein, 2013).

To identify the causes of infection, 16S RNA sequencing of sponge symbionts (Webster et al., 2002; Cervino et al., 2006; Angermeier et al., 2011; Stabili et al., 2012; Choudhury et al., 2015; Gao et al., 2015; Sweet et al., 2015; Blanquer et al., 2016), amplicon sequencing of other genome sites of bacteria and eukaryotes (Choudhury et al., 2015; Sweet et al., 2015), whole genome sequencing of a bacterial pathogen (Choudhury et al., 2014), and culturing of pathogenic bacteria (Stabili et al., 2012; Choudhury et al., 2015) were used in these studies. The significant changes in the composition of the microbiome were observed in all cases of sponge disease described. Only in some studies these experiments allowed identifying the pathogen or group of pathogens that caused sponge infections (Webster et al., 2002; Cervino et al., 2006; Stabili et al., 2012; Sweet et al., 2015), as well as biochemical mechanisms through which infection developed (Webster et al., 2002; Choudhury et al., 2015). However, in case of Baikal sponges disease, as in some other cases of sponge disease (Angermeier et al., 2011; Blanquer et al., 2016), such analysis was not effective enough to identify the cause of the disease.

3. Studies of the disease of the Baikal sponges

3.1. Field studies

In May-June 2015, 11 transects were laid throughout the water area of Lake Baikal: transects Nos. 1-3 – near Varnachka, transect No. 4 – Ulanovo settlement, transect No. 5 – near Olkhonskiye Vorota Strait, transect No. 6 – Cape Ukhan, transect No. 7 – Cape Elokhin, transect No. 8 – Cape Turali, and transects Nos. 9-11 – in the Listvennichny Bay. During annual expeditions around Lake Baikal, at these transects quantitative and qualitative collection of sponge samples was carried out. We have developed a new method, which allows us to take not the whole sponge, but only its small part, after which the sponge remains viable. In 2015, sponges were mapped using photo and video documentation, and approximately 1800 sponge samples were collected. The data obtained in 2015 were processed and published in the Journal of Great Lakes Research (Khanaev et al., 2018). Subsequently, similar expeditions with the collection of the sponge samples were conducted in 2016-2018. The diseased sponges were found throughout Baikal, but the degree and intensity of the disease varied depending on the lake areas and the depths. Percentage of the projective cover of the bottom by diseased and healthy sponges varied in the basins. Thus, the ratio of diseased sponges to healthy ones (1 m^2) in Southern Baikal Basin varied from 22.3 to 51.4%, in Central – 8.4-11%, in Northern – 8.5-11%. The data we obtained are basic for studying the dynamics of the state indicators of spongiofauna in the future.

3.2. Analysis of Baikal sponge metagenomes

The endemic freshwater Baikal sponges of the Lubomirskiidae family dominate the littoral zone of the lake, and their biomass is more than 700 g per m^2 (Kozhov, 1972; Pile et al., 1997; Semiturkina et al., 2009). Such sponge biomass is unusually high for the freshwater body (Bailey et al., 1995), but comparable to coastal Antarctic benthic communities (Dayton et al., 1974) and some reefs (Wilkinson, 1987). *L. baicalensis* has a rich green color due to the presence of a large amount of symbiotic green algae, probably *Choricystis* sp. (Trebouxiophyceae).

Fresh samples of sponges *L. baicalensis* were collected by scuba diving during field trips conducted in 2010, 2011 and 2015 from the Southern, Central and Northern Baikal Basins. The samples were frozen at -20 °C immediately after lifting and transported to the laboratory in refrigerator for subsequent DNA isolation and sequencing analysis.

Total DNA was isolated using TRIzol LS reagent (Invitrogen, Ambion, USA) according to the manufacturer's protocols. The universal bacterial primers 518F and 1064R (Huber et al., 2007) were used to amplify the V4–V6 hypervariable region of the bacterial 16S rRNA gene using the 454 GS Junior sequencing System and with GS FLX Titanium series reagents in Irkutsk Antiplague Research Institute of Siberia and the Far East. The raw sequencing reads are available under BioProject ID: PRJNA369024.

In the aggregate processing of data files obtained using two different sequencing technologies, an open-reference OTU picking implemented in the QIIME package (Caporaso et al., 2010) was used. Within the QIIME platform, the sortmerna_sumaclust option (Kopylova et al., 2016) was used as a method, and the subset of SILVA database gg_13_5 compatible with the Picrust package (Mukherjee et al., 2017) was used as a reference.

Fig.1 shows the distribution histogram of families of microorganisms in the sponge samples.

The analysis of the histogram indicated that the content of green alga (Trebouxiophyceae) in sponge samples varies greatly from 90 to 0%. At the same time, there was no clear correlation between the content of algae and the health of sponges. In sponges with external signs of the disease (see samples marked with purple blocks), the content of green algae could be comparable to a healthy sponge, as in 2010, decrease or disappear. Another family of crustal microbiome, the content of which varies significantly in different sponge samples, is *Chitinophagaceae*. The maximum number of these bacteria was observed in sponges without external signs of the disease, but with a reduced number of green algae. Sponges with an increased content of green algae relative to a healthy sponge in 2010, as well as sponges with a very low content of Trebouxiophyceae, had a low content of *Chitinophagaceae*. The remaining 5 families of the core microbiome did not change significantly, and the number fluctuations did not clearly depend on the health of the sponges. The bacteria *LD19* (*Verrucomicrobiaceae*) were an exception, the high content of which was found in a diseased pink sponge collected in 2011. Much smaller amounts of *LD19* were found in samples of healthy sponges collected in 2010 and 2011. Hence, a change in the composition of the microbiome may not lead to the appearance of external signs of the disease.

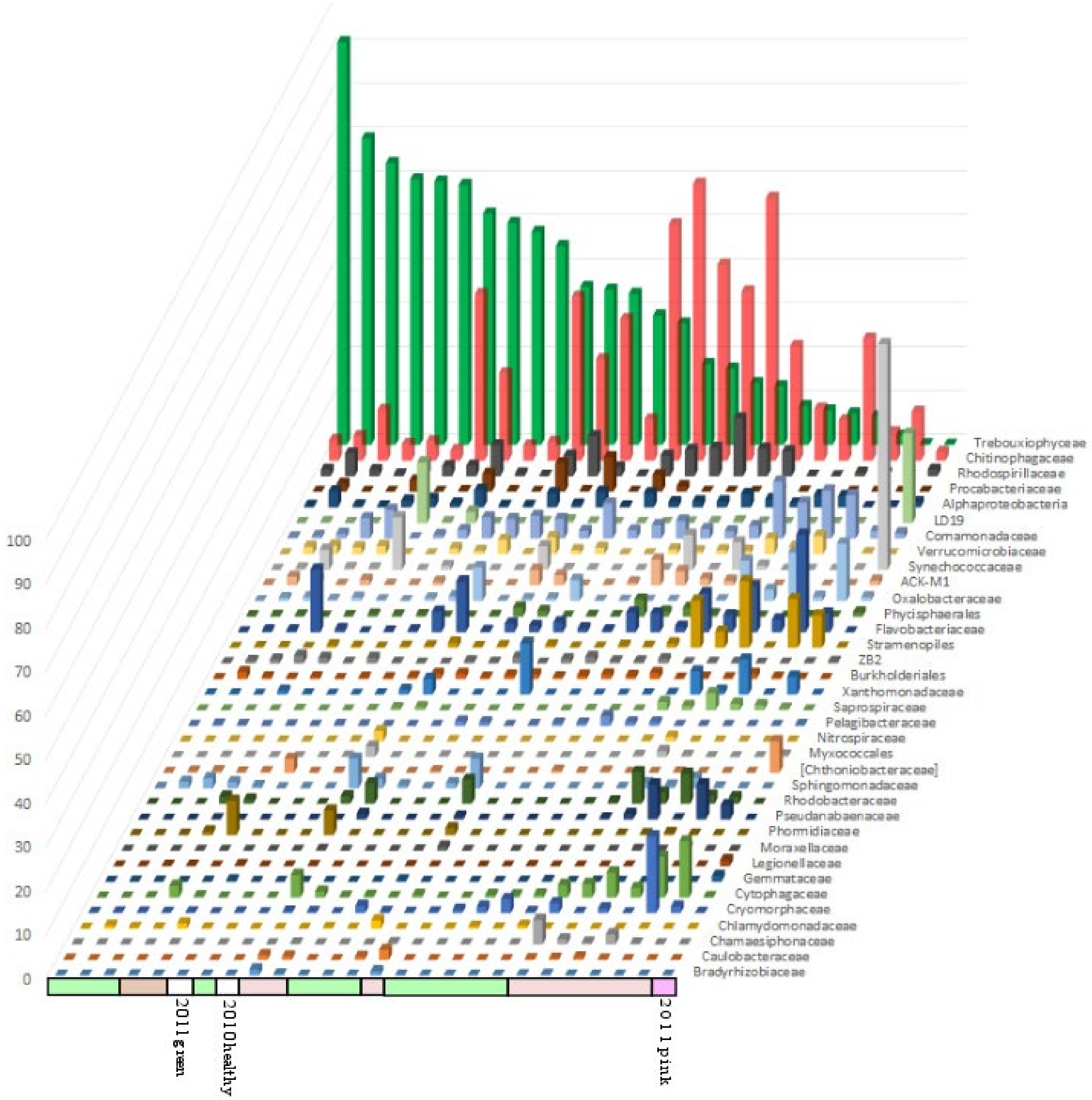

Fig. 1. The changes of the Baikal sponge microbiomes. The composition of microbiomes of Baikal sponges collected in 2015, ranked by reducing the amount of symbiotic green algae. Sponges with no visible signs of the disease are marked with a green rectangle; sponges with signs of the disease are purple. As a comparison, the compositions of microbiomes of a healthy sponge 2010 (2010 healthy), a diseased pink sponge 2011 (2011 pink) and a sponge without external signs of the disease 2011 (2011 healthy) are given. The analysis included families of bacteria whose content exceeds 0.5%.

4. Conclusion

Therefore, the composition of the microbiome in Baikal sponges differs from the microbiome of sea sponges, but the recorded changes in the microbiomes leading to dysbiosis are apparently not the cause of the disease. The most likely causes are stressful effects, such as rising temperatures, increasing concentrations of nutrients, and other unknown factors.

At the same time, ecological stress accompanied by changes in the symbiotic microbial community can lead not to death, but to the adaptation of the holobiont to new conditions (Webster and Reusch, 2017). Thus, symbiotic microorganisms of corals influence their ability to acclimate to the changing environmental conditions (Reshef et al., 2006; Ziegler et al., 2017). Changes in the genomes of microorganisms are possible, but they rarely occur, and speciation proceeds slowly. However, the composition of the sponge symbionts can rapidly change by capturing new microorganisms from the environment. Additionally, genetic changes in the associated microbiome are also possible, for example, by accelerating horizontal gene transfer (Thomas et al., 2010; Fan et al., 2012; Gao et al., 2014). Horizontal gene transfer can quickly result in acquisition of new functions without changes in taxonomic composition (Rosenberg et al., 2007; Putnam et al., 2017).

In recent years, some scientists engaged in microbiology of sponges have joined the project (The Sponge Microbiome project) in order to develop the standardized protocols and unified databases of the microbial diversity of symbionts in marine sponges (Thomas et al., 2016; Moitinho-Silva et al., 2017). Joining to this project may be reasonable to find causes of the disease of Baikal sponges. Comparison of diseases in marine and freshwater sponges is not only of practical, but also of theoretical interest to clarify the role of the host as the basis of the ecosystem and to determine mechanisms underlying the interaction between sponge and microorganisms. Therefore, a comparison of marine and freshwater holobionts can facilitate understanding of the relationship between the stress, dysbiosis and the disease or adaptation of sponges in order to develop a strategy for managing a situation.

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